Body Size in *Amblyrhiza inundata* (Rodentia: Caviomorpha), an Extinct Megafaunal Rodent from the Anguilla Bank, West Indies: Estimates and Implications

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ABSTRACT

Rodent species typically evolve larger mean body sizes when isolated on islands, but the extinct caviomorph *Amblyrhiza inundata,* known only from Quaternary cave deposits on the islands of Anguilla and St. Martin (northern Lesser Antilles), provides an unusually dramatic example of insular gigantism. Here we report on a series of body mass estimates for *Amblyrhiza* using predictive equations based on anteroposterior diameters and cortical cross-sectional areas of humeral and femoral diaphyses. Analyses of 14 isolated specimens (5 femoral, 9 humeral), all representing adult or near-adult animals, yield body mass estimates ranging from slightly less than 50 kg to more than 200 kg. Body size estimates derived from humeral measurements are lower than those derived from fem-

oral measurements, but the significance of this will remain unclear until matched limb bones (i.e., specimens from the same animal) are recovered. Incisor measurements are also highly variable, but in this case the distribution is demonstrably bimodal. Presence of multiple coeval species, temporal variation, limb heterogeneity, and sexual dimorphism all qualify as possible explanations of the variation encountered in *Amblyrhiza* data sets, but available samples are not adequate for making a robust choice among them. Body size affects many life history variables, including demography. Population estimates derived from empirical data and predictive equations suggest that only a few thousand individuals of *Amblyrhiza* could have occupied the islands of the Anguilla Bank at any

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one time during the Late Quaternary. At certain times—for example, during the last interglacial (Sangamonian) highstand—population numbers might have sunk to only a few hundred. Absolutely small population sizes of *Amblyrhiza* and severe fluctuations in island area during the late Quaternary surely affected its susceptibility to extinction, whether or not humans were ultimately responsible for the event (for which there is as yet no direct evidence).

INTRODUCTION

Anguilla, St. Martin, St. Barthélémy (St. Barths), and the flock of small islets and cays that lie near them in the northeastern Caribbean Sea constitute the subaerial parts of the Anguilla Bank (fig. 1). These landmasses (hereafter inclusively referred to as "Anguillea") have an aggregate area of only 215 km² and constitute one of the smallest archipelagos in the eastern Caribbean. It is therefore almost paradoxical that Anguillea should have uniquely supported, at least as recently as the Late Pleistocene, the largest island rodent ever discovered—*Amblyrhiza inundata* (fig. 2; Cope, 1869a, b). Just how large has been a matter of conjecture for more than a century. There are no European records pertaining to *Amblyrhiza,* and despite occasional statements to the contrary (e.g., Anderson, 1984), there is no basis for assuming that *Amblyrhiza* survived until European colonization. Indeed, it may have died out even before the Amerindian colonization (MacPhee et al., 1990), which occurred at least as early as 560 B.C. (2510 yr BP) in St. Martin (Haviser, 1991). Cope's (1869b: 184) original estimate, that it was larger than the "Virginia deer, and more than equalled the American Black Bear" has been dutifully repeated by later authors (e.g., McFarlane and MacPhee, 1989). This is not especially helpful, however, since *Odocoileus virginianus* and *Ursus americanus* exhibit great seasonal, sexual, and geographical variation (*O. virginianus,* 41–223 kg; *U. americanus,* 91–272 kg; Hazard, 1982)—a frequent pattern among continental megafaunal species. It is therefore of interest that *Amblyrhiza inundata* appears to have varied to a degree unmatched by any extant caviomorph, insular or continental (e.g., figs. 3, 6; table 4). This paper attempts to estimate body size and body size variation in *Amblyrhiza* in an analytically exacting manner and to relate these variables to inferences about its paleoecology.

ABBREVIATIONS

Institutional

AAHS	Anguilla Archaeological and Historical Society
AMNHP	American Museum of Natural History, Department of Vertebrate Paleontology
AMNHM	American Museum of Natural History, Department of Mammalogy
FMNH	Field Museum of Natural History
SUNY	State University of New York at Stony Brook
USNM	United States National Museum of Natural History

Measurements

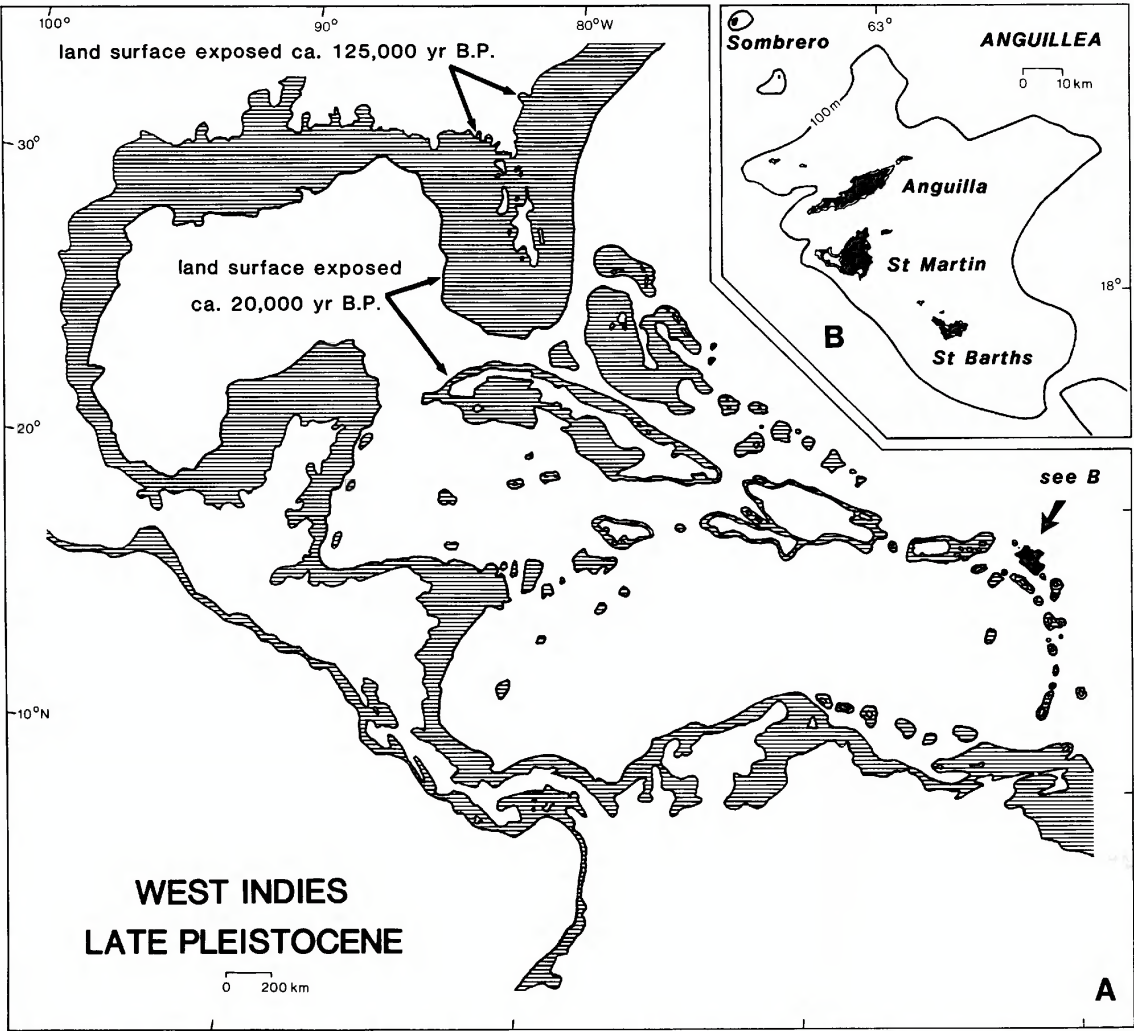|	
A	anterior
AP	anteroposterior

Fig. 1. Sketchmaps of the West Indies and adjacent continental areas comparing maximum and minimum exposures of land during the late Pleistocene, ignoring effects of uplift/subsidence (modified from MacPhee et al., 1989). In A, shaded areas correspond to land exposed at ca. 20 kyr BP (Wisconsinan pleniglacial), assuming a maximum depression of sea level of -118 m at this time (Bard et al., 1990). The inner border corresponds to assumed shore line at ca. 125 kyr BP (mid-Sangamonian). In B, outlines of modern shorelines are superimposed on the -100 m isobath of the Anguilla Bank, as depicted on American Geographical Society Map Sheet NE-20 (1:1,000,000). Shaded core of each island represents shorelines at 125 kyr BP assuming $+6$ m rise in sea level (e.g., Chen et al., 1991). At 20 kyr BP, Anguillea, defined as the continuous land area ringed by the -100 m isobath, would have been flanked by smaller (and now foundered) islands trending to the NW and SE. However, these would have been separated from Anguillea proper by straits deeper than -200 m and were therefore not included in the computation of the area of the terminal Wisconsinan landmass (~ 2500 km²).

CA	cross-sectional area	*Statistical Symbols*	
L	lateral	OLS	ordinary least squares regression
M	medial	r^2	coefficient of determination
ML	mediolateral	RMA	reduced major axis regression
P	posterior	SD	standard deviation

Fig. 2. Artist's reconstruction of a Late Quaternary scene on the south shore of Anguilla, with St. Martin in the distance and a pair of *Amblyrhiza inundata* in the foreground. Fossils of *Amblyrhiza* have only been recovered from cave sites on the two largest islands of the Anguilla Bank, Anguilla and St. Martin, although during times of lowered sea level populations presumably dispersed to other emergent parts of the Bank. Details of external appearance are conjectural, but the elongation and gracility of the forelimb compared to the seemingly disproportionately large size of the head, trunk, and hind limb are consistent with the fossil evidence, as is the suggestion of significant size variation among individuals. *Amblyrhiza* is probably most closely related to *Elasmodontomys obliquus* of Puerto Rico, a much smaller species also known only from Late Quaternary contexts. Larger sister-group relationships of these rodents are unclear, although both are conventionally placed in Heptaxodontidae (an undoubtedly paraphyletic grouping containing a variety of very large to gigantic caviomorphs from the Neogene of South America). [Painting by Dan Bruce; used with permission of the artist and the Centennial Museum of Kelowna, British Columbia, Canada].

$\bar{x}$	arithmetic mean
%PE	percent prediction error
95% CI	95% confidence interval

Other

BP	before present
kyr	thousand years

BODY MASS ESTIMATION

SPECIMENS AND MEASUREMENT TECHNIQUES

We define body size as body mass. For extinct animals, size has to be estimated from some other variable (usually osteological), preferably one that can be shown to be highly correlated with body mass in extant taxa (see Ruff, 1990). For example, bone lengths and external diaphyseal diameters are regularly chosen as estimators because they are readily measurable (e.g., Aiello, 1981; Gingerich, 1990), but their accuracy (especially across different locomotor groups) is not consistently high (Ruff, 1987). Differences in preferential planes of mechanical strength in diaphyses of different locomotor groups (see Burr et al., 1981; Demes and Jungers, 1989) will obviously complicate choosing any single diameter as an estimator, since the amount of cortical bone may be overestimated for one
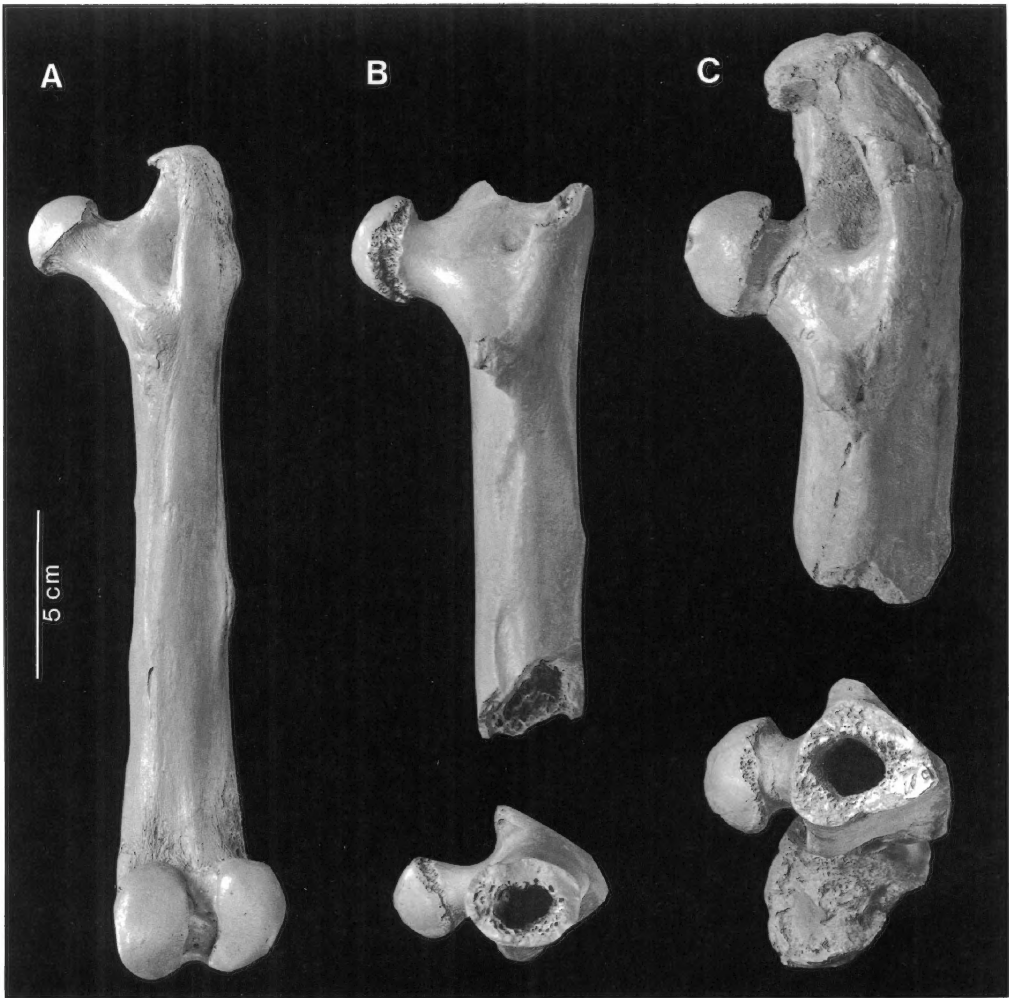
Fig. 3. "Small" (AMNHP 11847) and "large" (AMNHP 118430) proximal femora of *Amblyrhiza*, compared to femur of an extant *Hydrochaeris hydrochaeris* (AMNHM 209121), the largest living caviomorph, in posterior (caudal) aspect. Shaft fracture surfaces, also shown, illustrate variation in cortical thickness in the fossil taxon. The individual represented by AMNHP 11847 is estimated to have weighed ~ 74 kg, or somewhat more than mean body size of extant capybaras (~ 60 kg); AMNHP 118430, at ~ 168 kg, was more than twice as large (OLS estimate; see table 4).

group and underestimated for another. Furthermore, Bertram and Biewener (1990) demonstrated that external diameters may scale differently to bone length in small vs. large (> 100 kg) mammals. Because body mass estimates for some individuals of *Amblyrhiza* exceed 100 kg (see below), estimates derived from equations using AP diameters may be suspect. Finally, long-bone diaphyses are not solid and the relationship between cortical bone thickness and medullary cavity size can vary greatly between species (Currey and Alexander, 1985; Demes and Jungers, 1989; Biknevicius, 1993). Some of these difficulties with external diameters can be overcome by utilizing cortical cross-sectional areas (CA). Ruff (1987) has demonstrated that cortical CAs yield more accurate measures of body mass than do external diameters because cortical CA takes into account the actual amount of tissue in any section of bone. Unpaired limb bones (femora and humeri) are best for this purpose because they do not share weight-bearing functions with other

TABLE 1
Measurements of Femora and Humeri in Extant Caviomorph Rodents[a]

	N	W	Proximal femur		Distal humerus	
			AP	CA	AP	CA
Agoutidae						
Agouti paca	4	8.450	10.05	61.48	8.16	38.24
Caviidae						
Cavia sp.	5	0.564	3.72	8.80	2.92	4.18
C. aperea	3	0.438	3.50	8.40	2.93	3.60
Galea musteloides	6	0.274	2.67	4.13	2.28	2.42
Microcavia niata	1	0.260	2.50	4.88	2.22	3.41
Ctenomyidae						
Ctenomys opimus	7	0.392	2.91	7.60	2.96	5.23
Dasyproctidae						
Dasyprocta aguti	3	2.950	8.10	33.96	5.47	14.70
D. azarae	1	2.350	7.85	28.88	5.58	13.43
Echimyidae						
Dactylomys dactylinus	1	0.356	3.08	5.39	2.50	3.29
Isothrix bistriatus	1	0.340	3.45	6.15	2.50	3.34
Proechimys brevicauda	6	0.342	3.36	6.51	2.45	3.17
Proechimys sp.	2	0.358	3.30	6.27	2.12	2.54
Erethizontidae						
Coendou bicolor	2	4.250	7.33	36.72	6.45	22.73
C. prehensilis	7	4.249	7.85	38.40	7.71	27.45
Erethizon dorsatum	2	9.979	10.90	55.54	8.63	43.37
Hydrochaeridae						
Hydrochaeris hydrochaeris	2	49.900	21.13	285.31	19.76	167.33

[a] Anteroposterior diameters (AP) and cortical cross-sectional areas (CA) measured on the femoral shaft at 65% from its distal end and on the humeral shaft at 35% from its distal end. Body mass in kg; diameter in mm; area in mm^2.

bones in their limb segments. How (or whether) cortical CAs scale differently in large-bodied mammals is, as yet, unknown.

To estimate cortical CA, an approximation of actual cross-sectional shape is needed. Although cut sections will obviously provide the truest shapes (Ruff and Hayes, 1983), this approach is contraindicated for most museum osteological collections. Computed tomography (CT) has been used as a noninvasive technique for retrieving information about cross-sectional properties of bones (Jungers and Minns, 1979; Ruff, 1987), but commercially available CT equipment cannot yet resolve thicknesses that are < 1 mm (Runestad et al., 1993). In many mammalian groups (including the one of interest in this paper, caviomorph rodents), cortical thicknesses ≤ 0.5 mm are typical for smaller taxa. Still another approach to data collection, and the one utilized here, is standard radiography. Properly interpreted (Biknevicius and Ruff, 1992), radiographic images can provide

highly accurate approximations of cortical CAs. The limit of the method is that accuracy is highest when the chosen section presents relatively regular subperiosteal and endosteal perimeters of cortical bone; when perimeters are extremely irregular (as they are, for example, through the deltopectoral crest of the humerus), section reconstructions may be inaccurate and should be avoided. There is also a danger of recognizing artificially contracted endosteal perimeters in radiographs of fossil bones containing crystalline deposits or matrix-filled cancellous bone (Grine et al., 1989); in order to circumvent this problem, we used both cortical CAs and AP diameters in body mass estimations.

We focused on extant caviomorphs and collected data from 53 specimens representing 16 species (table 1; appendix). All specimens were wild-caught with field-recorded body mass, and all were adult except for specimens of *Hydrochaeris hydrochaeris,* for which only known-weight subadults were

available. *Amblyrhiza* is represented by rather poor material: although the AMNHP and AAHS collections include almost all known specimens, only five proximal femora and nine distal humeri of putatively adult animals were found which were sufficiently intact to measure (table 2). Suspected juvenile and subadult specimens (epiphyses not fused to diaphyses) were not used. Given the level of preservation and completeness, there was no way of reliably computing the minimum number of individuals represented by sampled elements. Except for teeth in the AAHS collection, which are cataloged by locality, exact provenance is usually unknown.

Each bone utilized for study was radiographed in AP and ML planes. Two sampling positions were selected, corresponding to a section taken at 35% of the total distance from the distal end of the humerus and another at 65% from the distal end of the femur (fig. 4; for additional details, see Biknevicius [1993]). These sites were chosen because they are represented in the fossils and because their external perimeters were regular in cross-sectional shape. At each section, four cortical bone thicknesses (anterior, posterior, medial, lateral) were measured directly from radiographs using Helios dial calipers accurate to 0.1 mm. External AP and ML diameters were measured at the same section positions.

Subperiosteal and endosteal perimeters were idealized as regular ellipses for section reconstruction. Cancellous bone was ignored in this analysis as its contribution to long-bone strength and rigidity was assumed to be negligible (Ruff, 1983). Cortical cross-sectional area was computed as:

$$\text{Cortical CA} = \text{TA} - \text{MA}$$
$$= [\pi \cdot \text{AP} \cdot \text{ML}/4]$$
$$- [\pi \cdot (\text{AP} - \text{A} - \text{P})$$
$$\cdot (\text{ML} - \text{M} - \text{L})/4],$$

where MA is medullary area (circumscribed by the endosteal perimeter of cortical bone) and TA is total subperiosteal area (assuming a solid ellipse, circumscribed by the subperiosteal perimeter). Other terms are listed in Abbreviations. Cortical CAs were unobtainable from three specimens (two femora, one humerus) in which cancellous bone was compacted with dense matrix, thereby obscuring the true endosteal perimeters.

TABLE 2
Measurements of Femora and Humeri of *Amblyrhiza*[a]

Specimen[b]	AP	CA
Femoral fragments		
AMNHP 11847	25.00	353.21
AMNHP 11843N	30.10	515.56
AMNHP 11843O	34.90	653.41
AMNHP 117527	37.00	—
AMNHP 108765	37.40	—
Humeral fragments		
AMNHP 11846C	20.54	164.54
AAHS 89037	21.64	222.29
AMNHP 11843A	22.14	201.18
AMNHP 117507	23.08	216.51
AAHS 91283	23.50	—
AMNHP 117530	24.81	286.43
AMNHP 117565	23.90	310.78
AMNHP 11848C	23.20	285.91
AMNHP 117541	24.35	314.08

[a] Anteroposterior diameters (AP) in mm; cortical cross-sectional area (CA) in mm^2.

[b] Femoral and humeral measurements were taken at locations that approximated those taken on the diaphyses of extant caviomorph bones.

REGRESSION ANALYSES

Ordinary least squares (OLS) and reduced major axis (RMA, model II) regressions were used to construct predictive equations for estimating body mass using AP diameters or cortical CA from proximal femoral and distal humeral sections. The data were log_{10}-transformed prior to running the regression analyses. OLS regression is generally recognized as the appropriate technique for predicting expected values (Ruff, 1987; LaBarbera, 1989; Damuth, personal commun.). But, since AP diameters and cortical CAs of the largest specimens of *Amblyrhiza* are half again as large as those of the largest extant species in the sample (table 2), extrapolation outside the observed range of caviomorph body mass was necessary for nearly all specimens. Extrapolation is potentially problematic, but we note that the caviomorph scaling relationship of femoral cortical CA to body mass does not differ significantly from that reported by Ruff (1987) for anthropoid primates ranging in size
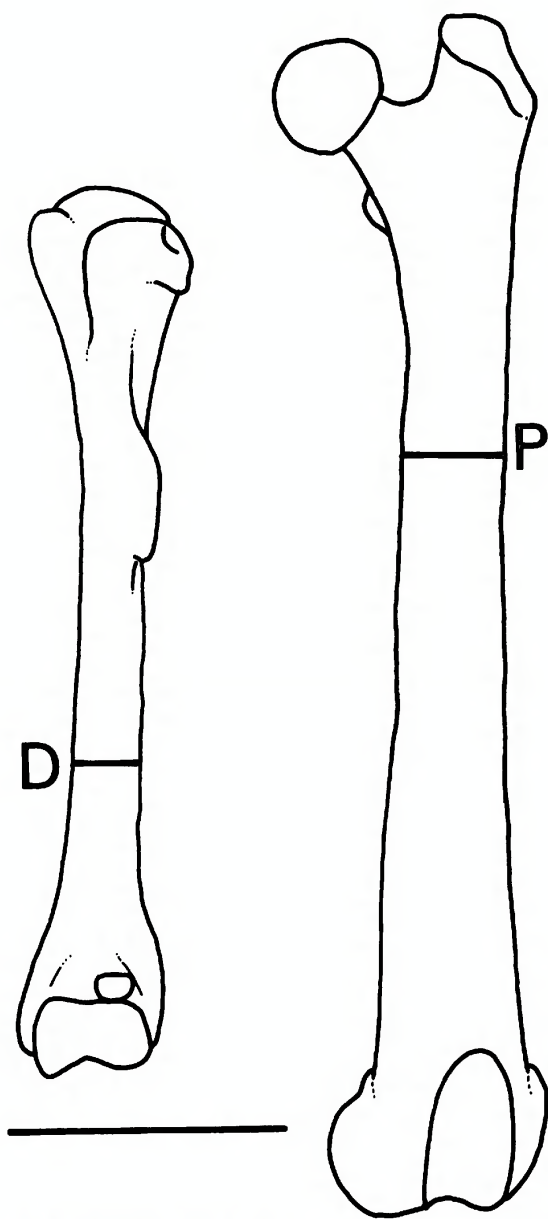
Fig. 4. Locations of sections reconstructed on the diaphyses of caviomorph femora and humeri. Species illustrated is *Proechimys brevicauda*. Sections: D, distal humeral sections located at 35% from the distal articular surface of the humerus; P, proximal femoral sections located at 65% from the distal articular surface of the femur. Scale bar = 1 cm.

from slightly more than 3 kg to nearly 170 kg. Our results are also comparable to those reported by Biewener (1982) for a mixed sample of even greater size range (35-g mouse to 276-kg horse). Use of RMA regression when extrapolation is required has been suggested (Ricker, 1973) and thus both methods of estimation are presented here. Comparisons of body mass estimates using OLS and RMA regression techniques and using independent variables (AP diameters and cortical CA) were performed via paired *t*-tests.

Although caviomorph rodents include species that are cursorial (*Dasyprocta*), fossorial (*Ctenomys*), and arboreal (*Coendou*), no attempt was made to scale functionally equivalent forms because no single specialized (or for that matter, generalized) locomotor habit has been assigned to *Amblyrhiza*. Although it would have been useful to judge the intuitive likelihood of our body weight estimates against extant analogs having plausibly similar locomotor activities or dietary preferences, in the absence of any useful functional studies of *Amblyrhiza* we had no basis for doing so.

The predictive power of the regression equations was assessed by coefficient of determination and percent prediction errors. The coefficient of determination (r^2) measures the percentage of total variability in the independent variable explained by variation in the dependent variable. Percent prediction errors (%PE) of the estimate were computed, after all parameters were converted to linear from log scale, according to the expression (Smith, 1984):

$$\%PE = [(\text{observed} - \text{predicted}) \div (\text{predicted})] \cdot 100$$

Both mean and absolute %PEs are reported.

ESTIMATES

Predictive equations generated using femoral and humeral cross-sectional parameters are listed in table 3. Nearly identical slopes for femoral and humeral regressions indicate that scaling relationships are similar across both sections sampled. Predictive equations constructed using proximal femoral data (either AP diameters or cortical CAs) are significantly different from equations based on humeral data, due principally to the greater elevations of the femoral regression lines (*P*

Independent variable (X)	Ordinary least squares		Reduced major axis		r^2	Mean %PE	Absolute %PE
	b	log a	b	log a			
AP Diameter							
Proximal Femur	2.518	−1.678	2.567	−1.712	0.964	4.21	22.37
Distal Humerus	2.484	−1.467	2.516	−1.486	0.970	2.99	20.25
Cortical CA							
Proximal Femur	1.327	−1.510	1.343	−1.530	0.975	3.21	18.71
Distal Humerus	1.262	−1.118	1.282	−1.136	0.969	2.95	19.19

[a] Data from table 1; all data $\log_{10}$-transformed. Statistics are for log W = log a + b(log X), where W is body mass (in kg), log a is intercept, b is slope, and X is independent variable (AP diameter, in mm, or cortical CA, in mm^2).

[b] r^2, coefficient of determination; %PE, percent prediction error.

< 0.001; table 3; fig. 5). This reflects the general tendency among caviomorphs (and many other mammals) for femoral sections to have greater AP diameters and cortical CAs than do humeral sections in the same animal (Biknevicius, 1993).

Measures of the predictive power of the OLS equations are listed in table 3. All equations have high values for r^2. Both mean and absolute %PE are similar in magnitude for the equations based on humeral data, but femoral %PEs are greater using AP diameters than using cortical CAs.

Estimates of body mass for *Amblyrhiza* are listed in table 4. Estimates derived from RMA regression equations are in all cases significantly larger than those derived from OLS regression equations ($P < 0.02$), but the difference is $\leq 10\%$. Body mass estimates using femoral AP diameters (~ 70–177 kg) range slightly, but insignificantly ($P > 0.06$), lower than estimates derived using femoral cortical CAs (~ 75–178 kg) where both estimates were obtainable. AP diameters in two particularly robust femora gave the greatest estimates (over 200 kg) but cortical CAs for these specimens could not be accurately determined. No difference was found in body mass estimates derived using humeral AP diameters (~ 62–101 kg) or humeral cortical CAs (~ 48–116 kg; $P > 0.86$). To put these estimates in a broader context, the smallest specimens of *Amblyrhiza* examined here were equal in estimated body mass to the adult mean for the largest living caviomorph, *Hydrochaeris*

(60 kg; Ojasti, 1973) whereas the largest were more than three times this last figure.[4]

VARIATION IN INCISOR TOOTH SIZE

The bewilderingly wide scatter of body mass estimates for *Amblyrhiza* yielded by the longbone data demands an explanation. First, however, it is important to determine whether there is any structure in the scatter, and in particular whether it conforms to a bimodal distribution. Identifying bimodality in osteological samples is frequently difficult, because the upper tail of one population or modal class may overlap the lower tail of the other (Godfrey et al., 1993). No long bone is represented in the *Amblyrhiza* collections in sufficient numbers to offer any hope of demonstrating a statistically significant bimodality, but the collections do include a relatively large number of incisor teeth adequate for the purpose. Few *Amblyrhiza* incisors are complete, but even small pieces can be accurately distinguished as belonging to maxillary or mandibular dentitions.

After separating upper and lower incisors and removing fragments clearly belonging to the same tooth (i.e., fragments with comple-

[4] These may be considered conservative body weight estimates since transformation from $\log_{10}$-predicted values (from the OLS regressions) to arithmetic units did not correct for detransformation bias (Smith, 1993); detransformed predictions may underestimate the target unknown by 5 to 8%.
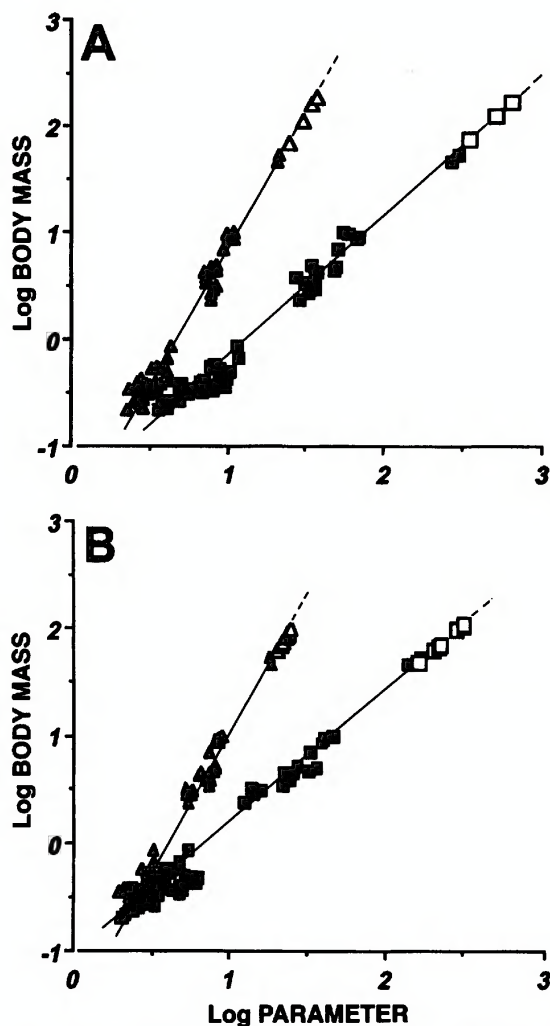
which duplicate identical widths were deleted, but statistics for this second set ($\bar{x} \pm$ SD = 11.476 $\pm$ 2.463; N = 59) are not significantly different from the first. However, since we have no check on the possibility that fragments of similar width may have come from different sites, it is appropriate to utilize the larger data set for analysis.

A simple frequency plot of 88 *Amblyrhiza* lower incisor widths is strongly suggestive of a bimodal distribution with modal peaks at 12–13 mm and 7–8 mm (fig. 7). On the basis of this assessment, specimens measuring 10 mm or larger were assigned to a "12 mm" class ($\bar{x} \pm$ SD = 12.6 $\pm$ 1.269; N = 65) and those measuring less than 10 mm were assigned to a "7 mm" class ($\bar{x} \pm$ SD = 7.5 $\pm$ 1.511). Expected frequencies for two normally distributed populations of these means and standard deviations were calculated and compared against the observed values using a chi-squared goodness-of-fit test. The distribution of *Amblyrhiza* lower incisor tooth widths does not significantly differ from a bimodal distribution of means 12.6 $\pm$ 1.269 and 7.5 $\pm$ 1.511 (chisq = 12.624; df = 10; P = 0.245). A chi-squared goodness-of-fit test of observed values against expected values drawn from a unimodal distribution ($\bar{x} \pm$ SD = 11.471 $\pm$ 2.379) demonstrates that the *Amblyrhiza* distribution is significantly different from a normal unimodal distribution (chisq = 40.342; df = 12; P < 0.001). The two very small teeth contributing to the small peak on the left tail in figure 7 are separately discussed below.

Fig. 5. Log-log plots of body mass (kg) on anteroposterior diameter (mm) and on cortical cross-sectional area (mm^2) for data from (A) the proximal femur and (B) the distal humerus. Triangles, AP diameters; squares, cortical CAs. Extant caviomorphs indicated by closed symbols; *Amblyrhiza* by open symbols.

INTERPRETATION OF SIZE VARIATION

Despite the small sample sizes of *Amblyrhiza inundata* available for interpretation, it seems that this taxon, as currently defined, was remarkably variable for metrical features of the long bones and incisors. Several explanations can be proposed to account for observed variability.

1. Multiple coeval species. From the vantage of modern ecological theory, it seems strange that one might infer merely from the variability in *Amblyrhiza* samples that the tiny islands comprising Anguillea could have simultaneously supported more than one

mentary fracture surfaces), we assembled a data set of 88 lower incisor tooth widths ($\bar{x} \pm$ SD = 11.297 $\pm$ 2.617). In general, individual *Amblyrhiza* incisors are uniform in width from the growing end to near the apical chisel (fig. 6). Accordingly, in the incisor sample it is possible, but not directly demonstrable, that fragments having similar widths (i.e., $\leq$ 0.01 mm difference) but no common fracture surfaces are from the same tooth. As a check, a second data set was developed, from

TABLE 4
Estimates of Body Mass for *Amblyrhiza* (in kg)[a]

Specimen	AP diameter		Cortical CA	
	OLS	RMA	OLS	RMA
Femoral fragments				
AMNHP 11847	69.50	75.25	74.29	77.98
AMNHP 11843N	110.93	121.29	122.80	129.60
AMNHP 11843O	161.00	177.19	168.17	178.15
AMNHP 117527	186.52	205.86	—	—
AMNHP 108765	191.64	211.62	—	—
Humeral fragments				
AMNHP 11846C	62.16	65.54	47.75	50.73
AAHS 89037	70.76	74.73	69.79	74.60
AMNHP 11843A	74.84	79.15	61.54	65.64
AMNHP 117507	83.04	87.88	67.31	72.12
AAHS 91283	86.84	91.96	—	—
AMNHP 117530	99.37	105.41	96.11	103.25
AMNHP 117565	90.56	95.95	106.53	114.64
AMNHP 11848C	84.15	89.04	95.89	103.01
AMNHP 117541	94.86	100.56	107.96	116.20

[a] Based on ordinary least squares (OLS) and reduced major axis (RMA) predictive equations using AP diameters or cortical CAs listed in table 3.

species of giant rodent. However, Cope (1868, 1869a, 1870, 1871, 1883) seemingly had no difficulty with this explanation: in his early papers he recognized four contemporaneous species of giant Anguillean rodents, distributed between two genera (later reduced to three species of a single genus). By modern standards, Cope's diagnoses of these taxa left much to be desired, and it is clear that size played the dominant role in his efforts to distinguish multiple species. Schreuder (1933) was aware of variation within *Amblyrhiza* but her sample size was too small to usefully explore it. Instead, she pointed out that morphological differences among Cope's nominal taxa were so trivial that only one species need be recognized—*A. inundata* as presently defined.

The seemingly continuous range of body mass estimates for *Amblyrhiza* derived from this study leads us to concur with Schreuder in rejecting the view that several closely related species of giant rodents occupied Anguillea simultaneously. However, the incisor width data present some evidence for the presence of a much smaller species. The minor peak on the far left of the graph in figure 7 is produced by two outlying variates, one of 3.7 mm (AAHS 90167) and one of 3.9 mm

(AAHS 90172). These lie more than four SDs below the mean of the remaining "7 mm" class ($\bar{x} \pm$ SD = 7.88 $\pm$ 0.995; N = 21). The probability of drawing two specimens of 3.9 mm or smaller from this adjusted size class is $\ll$ 0.0001. Similarly, there is a probability of 0.001 of finding two of 88 specimens with a width of 3.9 mm or less in a unimodal distribution of all other *Amblyrhiza* lower incisor widths ($\bar{x} \pm$ SD = 11.471 $\pm$ 2.379; N = 86). These results indicate that AAHS 90167 and 90172 cannot be assigned to *Amblyrhiza* and must represent some other taxon. *Rattus rattus* and *R. norvegicus* can be immediately excluded on the basis of size and total incisor length implied by the arc of curvature of the fragments. So can the species of *Megalomys* that existed until recently in St. Lucia, Martinique, and Barbuda, as can the unnamed extinct sigmodontine recently recovered by Steadman et al. (1984; M. D. Carleton, personal commun.) from cave deposits in Anguilla. By contrast, there is some degree of resemblance between the Anguillean specimens and the lower incisor of the agouti *Dasyprocta*. Agoutis were transported to the West Indies on several occasions by both Amerindians and Europeans (Hall, 1981), and agouti remains of unknown age
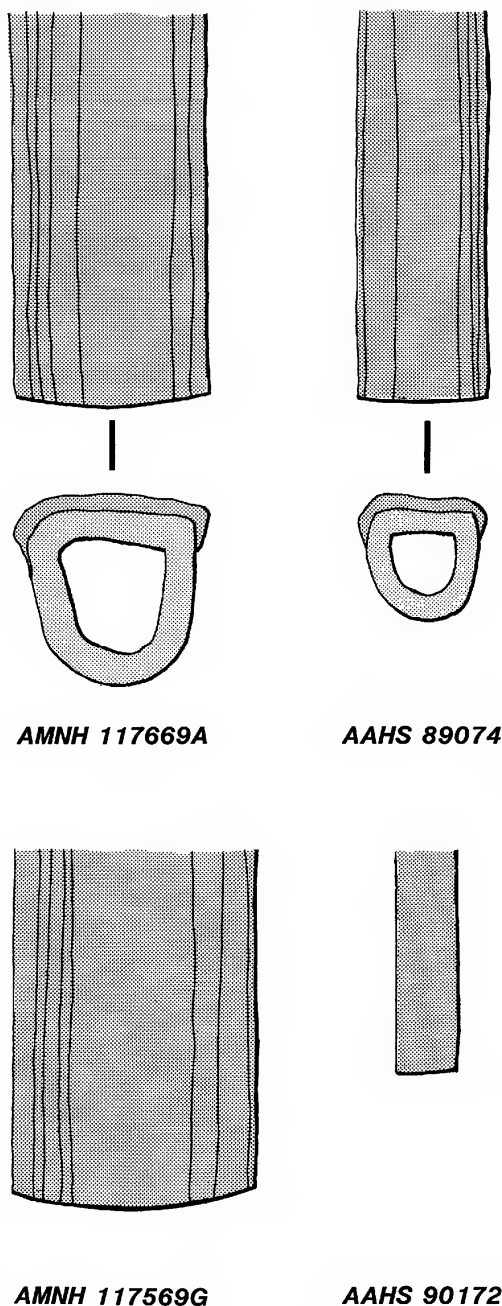
AMNH 117669A   **AAHS 89074**

AMNH 117569G   **AAHS 90172**

Fig. 6.   Variation in rodent mandibular incisor teeth from Anguillea. Drawings are schematic, but are based on the specimens indicated. AMNHP 117669A and AAHS 89074, shown in labial and cross-sectional views, have labial widths of 12.3 and 7.2 mm, respectively, and thus illustrate mean size differences between the "large" and "small" incisor classes described in the text. AMNHP 117569G (15.8 mm) and AAHS 90172 (3.9 mm) are representative of the largest and smallest teeth
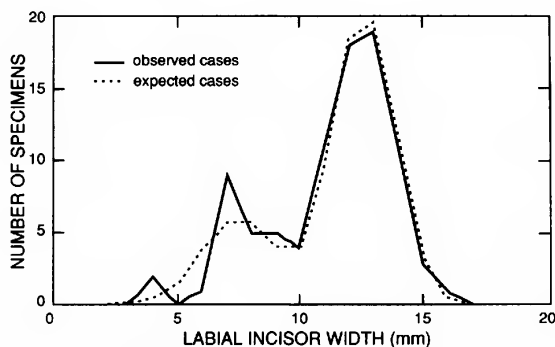

Fig. 7.   Frequency plot of lower incisor widths (mm). Major peaks, located at 12–13 mm and 7–8 mm, represent two size morphs of *Amblyrhiza*; the minor peak, located at ~ 3.8 mm, represents two specimens not assignable to *Amblyrhiza* (see fig. 6).

have been recovered from Tintamarre, a small island in the channel between Anguilla and St. Martin (MacPhee and McFarlane, unpubl.). In his monograph on Anguillean fossils, Cope (1883) described and figured bones that he believed were caviomorph. These elements are no longer in the AMNH Cope collection, but so far as we can determine from Cope's figures, they do not morphologically correspond to equivalent elements of any extant caviomorph. (The illustrated humerus, however, resembles that of a domestic cat.) If there was another endemic caviomorph resident in Anguillea, we have yet to find definitive evidence of it.

2. *Heterochroneity.* A second hypothesis is that the great size variability seen in *Amblyrhiza* may be due to unrecognized temporal variation.

It is now generally agreed that changes in body size—sometimes quite marked—occurred in a number of mammalian species

←

in the sample. AAHS 90172 differs from teeth assigned to *Amblyrhiza* not only in size but also in morphology: it lacks longitudinal ridges, characteristic of the enamel of the maxillary and mandibular incisors of *Amblyrhiza*. "Undescribed Species A" of Steadman et al. (1984), an extinct endemic sigmodontine, is too small to be the source of teeth in the size range of AAHS 90172. Incisors of *Dasyprocta leporina* are better matches, but allocation to this species is not supported here.

during the Quaternary (for an overview, see Kurtén and Anderson, 1980). In a few instances it is reasonably clear that size change occurred extremely rapidly. A good example is a population of red deer (*Cervus elephus*) that was isolated on Jersey, Channel Islands, during the last interglacial. Within a period of less than 6 kyr, as documented radiometrically, body size in the Jersey population decreased more than 80% (Lister, 1989). Similarly, relict populations of woolly mammoths (*Mammuthus primigenius*) on Wrangel Island displayed a 30% reduction in tooth size, and presumably body size, in 5–7 kyr (Vartanyan et al., 1993).

Heterochronous size change as an explanation for variability in *Amblyrhiza* cannot be usefully tested at present because a dense record of radiometric determinations is not available. However, the locality of Pitchapple Hole (Anguilla) has yielded specimens of both large and small size as has undated Tanglewood Cave (McFarlane and MacPhee, in prep.). None of the known *Amblyrhiza* localities is deeply stratified and, in our experience, *Amblyrhiza* bones are usually found lightly buried in cave sediments, generally within 40 cm of the surface. It may be additionally noted that the mammalian fossil records of nearby islands, such as Barbuda (Watters et al., 1984) or even Puerto Rico (MacPhee and Wyss, 1990), are exclusively Quaternary and therefore shed no light on the origin or time of emplacement of *Amblyrhiza* (or its ancestor) in Anguillea. At present, heterochronous sampling does not seem to be the best explanation for the enormous variation in *Amblyrhiza*.

3. Limb heterogeneity. Humeral diaphyseal construction in most (nonburrowing) caviomorphs is relatively gracile compared with that of the femur (Biknevicius, 1993). It is conceivable that *Amblyrhiza* may have taken a common pattern to an uncommon extreme as it appears to have had gracile, elongate forelimbs and massive hind limbs (see fig. 2). This might explain why weight estimates based on femora are, on average, greater than those based on humeri. The significance of limb heterogeneity for explaining variability in *Amblyrhiza* will have to await the discovery of forelimbs and hind limbs of single individuals.

4. Sexual size dimorphism. The final explanation that we shall consider is that the kind of variation seen in *Amblyrhiza* is due to the influence of sex on body size (see Godfrey et al., 1993). As a group, extant caviomorphs evidence very little sex-based dimorphism (ratio of male to female body mass: $\bar{x} \pm SD = 1.10 \pm 0.18$; $N = 32$; $\bar{x}$ not significantly different from 1, $P > 0.5$; table 5). Although animals of larger body size tend to display greater sexual dimorphism than do smaller animals (Reiss, 1989), larger caviomorphs are not more dimorphic than smaller ones; the RMA regression slope of female body mass on male body mass, both $\log_{10}$-transformed, is not significantly different from 1 (slope $\bar{x} = 1.031$; 95% CI = 0.990–1.074). However, some insular populations of nonrodent species have been found to be more sexually dimorphic than mainland populations (Selander, 1972; Schoener, 1977; Giannico and Nagorsen, 1989). If sexual dimorphism were used to explain its size variability, *Amblyrhiza* would be one of the most dimorphic terrestrial mammals known, with a 4:1 ratio of estimated weights (by cortical CA method) of largest to smallest animals.

A characteristic of sexual dimorphism is bimodal size distribution, but sample sizes are too low to demonstrate bimodality in the limb bone sample. This limitation does not apply to the incisor data, however, in which variates are clearly distributed in a bimodal manner (see Variation in Incisor Tooth Size; fig. 7). This, however, is really the only positive evidence for sexual size dimorphism in *Amblyrhiza,* beyond the fact (noted under Heterochroneity) that large and small elements (including teeth) have been documented at the same thinly stratified sites.

MECHANISMS LEADING TO GIGANTISM IN *AMBLYRHIZA*

Although it is a frequent pattern for rodents to become somewhat larger on islands (see Case, 1978), the scale of the size increase of *Amblyrhiza* compared with any likely ancestor is out of proportion to patterns encountered in other island rodents. Most of the literature on size contrasts between continental and insular mammal taxa concerns change in the opposite direction, toward

TABLE 5
Body Mass of Male and Female Caviomorph Rodents (in kg)[a]

Taxon	Male	Female	Ratio[b]	Source[c]
Agoutidae				
Agouti paca	7.650–9.350	6.500–9.100	1.102	7, 14
Capromyidae				
Geocapromys ingrahami	0.613–0.754	0.660–0.739	1.020	5, 6, 13
Myocastor coypus	4.230–8.160	4.700–7.938	0.995	2, 4, 11, 12, 26
Caviidae				
Cavia aperea	0.372–0.450	0.341–0.435	1.046	8, 16, 25
Galea musteloides	0.216	0.205	1.054	25
Chinchillidae				
Lagidium peruanus	1.220	1.252	0.974	18
Ctenomyidae				
Ctenomys opimus	0.439	0.284	1.546	19
Ctenomys peruanus	0.562	0.462	1.216	19
Ctenomys talarum	0.176–0.186	0.123–0.128	1.442	20
Dasyproctidae				
Dasyprocta leporina	3.418	3.825	0.894	14
Echimyidae				
Proechimys brevicauda	0.390	0.347	1.124	9
Proechimys guyannensis	0.330	0.302	1.093	10
Thrichomys apereoides	0.335	0.211	1.588	16
Erethizontidae				
Coendou prehensilis	4.510	4.980	0.906	22
Erethizon dorsatum	5.760–6.430	5.540–5.940	1.087	3, 15, 24
Hydrochaeridae				
Hydrochaeris hydrochaeris	41.800–57.57	36.800–51.900	1.079	1, 17, 23
Octodontidae				
Spalacopus cyanus	0.091	0.089	1.022	21

[a] Sources reporting *both* male and female body mass were used; data listed are means or ranges of means.

[b] Ratio equals male body mass divided by female body mass.

[c] Sources: 1, Alho et al., 1987; 2, Atwood, 1950; 3, Brander, 1973; 4, Brown, 1975; 5, Clough, 1972; 6, Clough, 1974; 7, Collett, 1981; 8, Deansely and Rowland, 1936; 9, Emmons, 1982; 10, Everard and Tikasingh, 1973; 11, Gosling, 1977; 12, Gosling, 1980; 13, Howe and Clough, 1971; 14, Husson, 1978; 15, Krefting et al., 1962; 16, Mares et al., 1989; 17, Ojasti, 1973; 18, Pearson, 1948; 19, Pearson, 1959; 20, Pearson et al., 1968; 21, Reig, 1970; 22, Roberts et al., 1985; 23, Schaller, 1983; 24, Shapiro, 1949; 25, Weir, 1970; 26, Wilson and Dewes, 1962.

dwarfing (e.g., Heaney, 1978; Vartanyan et al., 1993). *Amblyrhiza* may not be a sole outlier among island mammals in having evolved very large body size, but there are few comparable examples of equivalent scale. Several of the "subfossil" lemurs of Holocene Madagascar were enormous compared to their close relatives (e.g., *Megaladapis edwardsi*, which attained a body size equivalent to that of a female gorilla [Jungers, 1978]). However, at approximately 600,000 km², Madagascar has both the size and biotic diversity of a minicontinent (Burney and MacPhee, 1988), and in such a context the appearance of giant species is unexceptional. Anguilla, by contrast, is unfavorably placed with respect to

the currently dominant pattern of precipitation in the West Indies, receiving only 1040 mm of rainfall annually (Harris, 1965). The modern flora largely consists of an impoverished selection of xerophytic, scleophyllous species composing an evergreen bushland (Howard and Kellog, 1987). Whether this is a natural formation or due to anthropogenic alteration of the original flora is debated (Howard and Kellog, 1987), but it is hard to imagine that the floristic aspect of this island would have been dramatically different during the late Pleistocene when the West Indies were cooler and drier than they are today (Pregill and Olson, 1981). Accordingly, in addition to other imponderables about the evo-

lution of large body size in *Amblyrhiza,* one is also forced to contemplate that this evolution took place in what can only be regarded as a very marginal environment for a large herbivore. Understanding of this problem could progress further if there were a paleoenvironmental record for this island, preferably one based on palynological analyses. To spark interest on this point, we will briefly note that there are several allegedly permanent "ponds" in inland Anguilla, apparently fed by karst circulation, that may be worth testing as possible coring sites. In addition, there are also large speleothems in a number of Anguillan caves that might be profitably studied using the method of Brooks et al. (1990).

In any case, the great body size of *Amblyrhiza* does not appear to be a response to any recognizable form of competition: the largest endemic Anguillean herbivores (see table 6) are only a fraction of any reasonable estimate of *Amblyrhiza*'s body mass. Nor does it appear to be due to some form of predation, inasmuch as there are no faunivores represented in the known Anguillean Quaternary fossil record that would have been capable of subduing even a juvenile *Amblyrhiza.* However, several very large raptors existed in the West Indies during the Quaternary, where they filled predator niches unoccupied by mammalian carnivores (Olson, 1978). Some of these may have been capable of preying upon *Amblyrhiza,* although there are as yet no fossils that would demonstrate their presence in Anguillea.

DEMOGRAPHIC IMPLICATIONS

It is of interest to have an estimate of the probable instantaneous population density of *Amblyrhiza* on the islands of the Anguilla Bank. Predictions of population density in extinct mammals have been reported previously by Martin (1981, 1986). In table 7 we report on different approaches to the estimation of this parameter for herbivores (we assume that *Amblyrhiza* was a 'typical' herbivore and was not choosing an omnivorous strategy which might have increased its population density [Bodmer, 1989]). The first three entries in the table utilize OLS equations developed by other researchers for various herbivore samples (Damuth, 1981, 1987;

Peters and Raelson, 1984), in which body mass is regressed against local population densities to yield an estimate of individuals km^{-2}. The last entry utilizes an OLS equation we developed specifically for caviomorph rodents, using body mass and density data from the literature (table 8). In spite of differences in the predictive equations listed in table 7, no statistically significant differences were found when RMA regression coefficients were compared (see LaBarbera, 1989).

It is important to note that published densities can be misleading if, as is very often the case, actual population densities are well below reported population densities (Brown and Mauer, 1987, 1989; Lawton, 1989; Blackburn et al., 1990). Capybaras, for example, have been reported in densities as high as 247 animals km^{-2} (Cordero and Ojasti, 1981), an astoundingly high figure only because of near-optimum local conditions (no or low predation, except by humans; dependable and abundant food and water supply; setting allowing for dispersal at poor times). Much lower densities are the recorded norm (table 8); presumably, even lower densities obtain at places where animal numbers are so low that censusing is not considered worthwhile. We suspect that the estimated population densities for *Amblyrhiza* are, if anything, overestimates of the actual densities.

In table 7, a series of population density estimates are presented for *Amblyrhiza* using the largest and smallest weight estimates for *Amblyrhiza* (178 and 47 kg) developed from the analysis of cortical CAs. Relatively low densities were found with all equations used. The largest specimen yielded values of 0.7 to 2.4 individuals km^{-2}, while the smallest yielded 1.5 to 6.2 individuals km^{-2}. Extant caviomorphs living at similar densities to the ones estimated for *Amblyrhiza* include some dasyproctids, erethizontids, and hydrochaerids—in other words, taxa characterized by large body sizes.

At single points in time, islands have finite sizes available for exploitation by terrestrial mammals. Through time, however, island size can vary greatly in response to the local tectonic regime (producing net uplift or subsidence), sea level change, and other factors.

TABLE 6
Nonavian Vertebrate Fauna of the Large Islands of Anguillea (including Sombrero)[a]

	SOM	ANG	StM	StB
AMPHIBIA				
Salienta				
Leptodactylidae				
Eleutherodactylus johnstonei		+	+	
E. martinicensis				*
REPTILIA				
Sauria				
Gekkonidae				
Hemidactylus mabouia		*	*	
Thecadactylus rapicauda	+	+	+	+
Sphaerodactylus sputator	+	+	+	+
Sphaerodactylus macolepis		+	+	+
Iguanidae				
Iguana delicatissima		+	+	+
Anolis wattsi		+	+	+
Anolis gingivinus	+	+	+	+
Leiocephalus ?cuneus		(+)		
Teiidae				
Ameiva corvina	+			
Ameiva plei		+	+	+
Scincidae				
Mabuya maboya		+	+	+
Serpentes				
Colubridae				
Alsophis rijersmai		+	+	+
CHELONIA				
Testudinidae				
Geochelone sombrerensis	+			
Geochelone carbonaria		+[b]	+	
MAMMALIA				
Chiroptera				
Natalidae				
Natalus stamineus		+		
Noctilionidae				
Noctilio leporinus			+	
Phyllostomidae				
Artibeus jamaicensis		+	+	?
Monophyllus plethodon		+	?	?
Brachyphylla cavernarum		+	+	+
Molossidae				
Tadarida brasiliensis		?	+	+
Molossus molossus		+	+	?
Vespertilionidae				
Myotis ?nigricans			+	
Rodentia				
Heptaxodontidae				
Amblyrhiza inundata		(+)	(+)	
Dasyproctidae				
Dasyprocta aguti		(?)	(*)	*
Cricetidae				
Undescribed species A		(+)		
Muridae				
Rattus spp.		*	*	*
Mus musculus		*	*	*

TABLE 6—(*Continued*)

	SOM	ANG	StM	StB
Carnivora				
Herpestidae				
Herpestes auropunctatus			*	*

[a] Abbreviations: SOM, Sombrero; ANG, Anguilla; StM, St. Martin; StB, St. Barthélémy. Symbols: +, present; ?, possibly present; *, introduced by humans. Symbols in parentheses indicate locally or completely extinct taxa. Names and distributions of amphibians, reptiles, and chelonians as provided in Lazell (1972), Schwartz and Thomas (1975), Watters et al. (1984), Schwartz and Henderson (1985), and Censky (1989); other herpetological taxa may have existed until recently on Anguillean islands but their presence needs to be confirmed (see Roughgarden [1991] and taxon lists therein). Mammal distributions follow Baker and Genoways (1978), Steadman et al. (1984), Hoagland et al. (1989), Jones (1989), and Koopman (1989); *Dasyprocta* recorded on St. Martin is actually from Tintamarre (MacPhee and McFarlane, personal obs.). Some taxon records mentioned by Cope (1868, 1869a, b, 1870, 1871, 1883) are unconfirmed or spurious and are listed here (e.g., "deer," actually a domestic goat; "crocodile," unconfirmed [possibly sea turtle]).

[b] *Geochelone carbonaria* has been recognized in samples from Tanglewood Cave, and apparently occurred naturally in Anguilla prior to human arrival; see Lazell (in press).

The islands of the West Indies are not known to have experienced dramatic tectonic readjustments during the Late Quaternary, but they have certainly waxed and waned in size in response to glacially mediated sea level change during this time period (fig. 1). For this reason, it is important to develop several estimates of population size for *Amblyrhiza*. In table 9, population estimates are presented for land areas at three benchmark dates (0 yr [= Recent], 20 kyr, and 125 kyr BP). Sea level has varied slightly during the Recent, but not enough either to unite or markedly modify the size of the six largest islands on the Anguilla Bank (Anguilla, St. Martin, St. Barthélémy, Tintamarre, Dog Island, and Scrub Island). These islands could have maximally supported 1300 *Amblyrhiza* if average body mass was small (47 kg), but less than 600 individuals if it was large (178 kg). Modeled population sizes could be adjusted by assuming specific mixtures of body sizes (reflecting sexual or individual variation), but this would not alter the chief conclusion: assuming our methods of estimating population size are realistic, at no time during the last 10 kyr could the islands of the Anguilla Bank have supported more than a few thousand *Amblyrhiza*.

Total area available for occupation would have been quite different at the next benchmark, 20 kyr BP, the currently accepted focal date for the last glacial maximum. With sea level depressed in excess of 100 m, the land exposed on the Anguilla Bank would have comprised a single land mass, approximately 2500 km[2] in area.[5] Estimates of maximum population sizes for *Amblyrhiza* at this time range from over 15,000 to about 6000 for small- and large-size individuals (table 9).

[5] Woods (1989: 756) gave a figure more than twice this size (5949 km[2]) for the size of the Anguilla (his St. Martin) Bank "at times of low sea levels during the Pleistocene." Unless the Anguilla Bank has oscillated vertically during the Quaternary, for which there is no geological evidence (see Budd et al., 1989), sea level would have to be depressed by nearly 500 m to achieve Woods' estimate of platform exposure.

TABLE 7
Predictive Equations for Population Densities[a]

Equation[b]	b	log a	r	Population densities	
				47 kg	178 kg
1	−0.70	3.71	−0.86	2.8	1.1
2	−0.56	1.11	−0.67	1.5	0.7
3	−0.70	4.06	−0.80	6.2	2.4
4	−0.93	2.20	−0.56	4.4	1.3

[a] Equations established by OLS regressions on $\log_{10}$-transformed data. Coefficients are for log D = log a + b(log W), where D is density (in individuals km^{-2}), log a is intercept, b is slope, W is body mass, and r is correlation coefficient.

[b] Source of equations: 1, Damuth (1981) on worldwide herbivores (W in g); 2, Peters and Raelson (1984) on tropical and Central American herbivores (W in kg); 3, Damuth (1987) on South and Central American herbivores (W in g); 4, this study (data listed in table 8) on caviomorph rodents (W in kg).

TABLE 8
Body Mass and Population Densities for Extant Caviomorph Rodents[a]

	Body mass	Population density	Source[b]
Agoutidae			
Agouti paca	7.75–9.0	3.5–93	5, 7, 8, 19
Capromyidae			
Geocapromys ingrahami	0.698–0.707	3000	4
Caviidae			
Cavia aperea	0.827	3870	17
Galea musteloides	0.406	440	17
Microcavia australis	0.303	3020	17
Ctenomyidae			
Ctenomys opimus	0.362	247	15
C. peruanus	0.512	4199	15
Dasyproctidae			
Dasyprocta aguti	2.0	1.5–63	7
D. punctata	2.0–4.0	0.9–150	8, 12, 18, 19, 20
Myoprocta pratti	0.5–1.5	4–5.3	8, 20
Echimyidae			
Echimys semivillosus	0.2	17.2	7
Proechimys guyannensis	0.316	1057	10
P. semispinosus	0.3–0.5	126–220	7, 11
Erethizontidae			
Coendou bicolor	2.0	1	12
C. mexicanus	3.5	15	9
C. prehensilis	2.6–5.0	3.5–100	3, 7
Erethizon dorsatum	5.85–6.45	9.2–15.9	2, 16
Hydrochaeridae			
Hydrochaeris hydrochaeris	39.3–54.38	0.3–287	1, 6, 7, 8, 18
Octodontidae			
Octodon degus	0.156–0.215	3900–25,900	13, 14

[a] Body mass in kg; population density in number of individuals km^{-2}; data listed are means or ranges of means.
[b] Source: 1, Alho et al., 1987; 2, Brander, 1973; 3, Charles-Dominique et al., 1981; 4, Clough, 1972; 5, Collett, 1981; 6, Cordero and Ojasti, 1981; 7, Eisenberg et al., 1979; 8, Emmons, 1987; 9, Estrada and Coastes-Estrada, 1985; 10, Everard and Tikasingh, 1973; 11, Fleming, 1971; 12, Hendrichs, 1977; 13, LeBoulengé and Fuentes, 1978; 14, Meserve et al., 1984; 15, Pearson, 1959; 16, Randall, 1971; 17, Rood, 1972; 18, Schaller, 1983; 19, Smythe et al., 1982; 20, Terborgh, 1983.

The third benchmark is placed in the middle of the last (Sangamonian) interglacial, when land area would have been somewhat less than at present due to a ~6 m rise in sea level between 120 and 130 kyr BP (Chen et al., 1991; but see Lambeck and Nakada, 1992). If we take ~ 190 km² as a fair estimate of subaerial exposure on the Anguilla Bank at 125 kyr, Amblyrhiza may have been reduced to several fragmented populations of a few hundred animals each.

These estimates could be impugned on various grounds (e.g., use of estimated body mass to calculate population densities compounds the errors of the second analysis with that of the first; Martin, 1990), but unless one argues that all available models of density packing are inappropriate for Amblyrhiza, it is hard to avoid the conclusion that there were few times during the Quaternary that Amblyrhiza could have existed in large numbers, given inherent space limitations in its only known habitat. Sea level has rarely been stable for long periods during the past 125 kyr (Chen et al., 1991), and, given the new evidence for sudden iceberg (Bond et al., 1992) and meltwater (Bard et al., 1990) surges, there may have been flooding events of very brief duration that are not reflected in "average" estimates of highstands. In any case, it is cer-

	Hypothetical land masses[b]			
	Recent Anguilla (0 yr BP)	Recent Anguillea (0 yr BP)	Pleniglacial Anguillea (20 kyr BP)	Sangamonian Anguillea (125 kyr BP)
Equation 1:				
Maximum	218	602	7000	532
Minimum	86	237	2750	209
Equation 2:				
Maximum	117	323	3750	285
Minimum	55	151	1750	133
Equation 3:				
Maximum	484	1333	15,500	1178
Minimum	187	516	6000	456
Equation 4				
Maximum	343	946	11,000	836
Minimum	101	280	3250	247

[a] Derived using predictive equations and population estimates given in table 8. Estimated maximum and minimum population sizes for communities of *Amblyrhiza* composed exclusively of small (47 kg) and large (178 kg) individuals, respectively. Population size in number of individuals.

[b] Land masses: Recent Anguilla, ~ 78 km^2; Recent Anguillea, sum of all major land areas of the islands on the Anguilla Bank at their current size, ~ 215 km^2; Pleniglacial Anguillea, portion of Anguilla Bank above −100 m isobath (equivalent to area exposed ca. 20 kyr BP), ~ 2500 km^2; Sangamonian Anguillea, equivalent to area exposed ca. 120–130 kyr BP, ~ 190 km^2.

tainly justified to conclude that *Amblyrhiza* populations were repeatedly pushed through bottlenecks of fairly short duration.

At present, there is no definitive evidence as to the timing of the final population crash that culminated in the extinction of *Amblyrhiza*. It is usually assumed that people were the causative agent (e.g., Anderson, 1984), but no *Amblyrhiza* remains have turned up in the archaeological record which now extends well into the second millennium B.C. in St. Martin and even earlier on other islands in the Lesser Antilles (Haviser, 1991; D. Watters, 1991, personal commun.). A tool made from the shell of *Strombus gigas,* described by Cope (1883) as coming from one of the "bone caves" yielding *Amblyrhiza*, and therefore seized upon as evidence that hu-

mans were coeval with the giant rodent, is of unknown association, stratigraphic position, and provenance, and it has not been dated radiometrically. Its current interpretative value is therefore nil. Our own efforts to directly date remains of *Amblyrhiza* have yielded ambiguous results. To date, no sample of *Amblyrhiza* bone submitted for ^{14}C dating has contained a high enough fraction of organic material to permit reliable analysis (M. Tamers, personal commun.). Some mass spectrometric uranium-series (U/Th) determinations are now available for certain *Amblyrhiza* sites and will be published elsewhere. However, most of these dates are considerably older than any likely date for the arrival of Amerindians in the West Indies (see Burney et al., in press). In short, if people were in some way responsible for the extinction of *Amblyrhiza*, there is no evidence that reflects this.

CONCLUSIONS

Recent excavations in the cave deposits of Anguilla, British West Indies, have yielded new specimens of the enigmatic giant rodents first described by Cope in the late 19th century. Analysis of metrical variation in these specimens and in Cope's original material leads us to concur with Schreuder (1933) in recognizing only a single taxon of megafaunal rodent from the islands of the Anguilla Bank, albeit one which exhibits a remarkable range in body size (~ 50 to 200 kg, depending on method of analysis). There is an indication of bimodality in incisor widths, which could be consistent with sexual size dimorphism in *Amblyrhiza inundata*. However, it is not yet possible to falsify the hypothesis that size variation is actually a reflection of heterochroneity.

A definitive account of the extinction of *Amblyrhiza* is not yet possible. Nevertheless, more than 120 years of intermittent investigation have failed to turn up a single, unequivocal example of co-occurrence of *Amblyrhiza* and anthropogenic remains or artifacts. Estimates of *Amblyrhiza* population based on models of extant herbivore densities strongly suggest that *Amblyrhiza* would have suffered extreme demographic stresses during episodes of sea level highstands. In the ab-

sence of any fossil evidence for the persistence of *Amblyrhiza* into the Holocene, we suggest that late Quaternary sea level change is the most attractive explanation for the extinction of this extraordinary animal.

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APPENDIX I

Specimens of Extant Caviomorphs Used in this Study

Agouti paca (N = 4; AMNHM 143082, 134086, 134087, 143096)

Cavia sp. (N = 5; AMNHM 206411, 206421, 206424, 206429, 214620)

Cavia aperea (N = 3; AMNHM 134117, 134123, 134125)

Galea musteloides (N = 6; AMNHM 262993, 262994, 262997, 262998, 262999, 263001)

Microcavia niata (N = 1; AMNHM 263000)

Ctenomys opimus (N = 7; AMNHM 244655, 260839, 260841, 263036, 263038, 263047, 263050)

Dasyprocta aguti (N = 3; AMNHM 134158, 134160, 134175)

Dasyprocta azarae (N = 1; AMNHM 134157)

Dactylomys dactylinus (N = 1; AMNHM 210356)

Isothrix bistriatus (N = 1; AMNHM 210353)

Proechimys brevicauda (N = 6; AMNHM 214662, 214682, 214683, 214689, 214691, 247907)

Proechimys sp. (N = 2; AMNHM 210348, 214665)

Coendou bicolor (N = 2; AMNHM 214610, 214611)

Coendou prehensilis (N = 7; AMNHM 134064, 134067, 134069, 134070, 134073, 214613, 214614)

Erethizon dorsatum (N = 2; AMNHM 150093, FMNH 124114)

Hydrochaeris hydrochaeris (N = 2; AMNHM 214624, 214635)